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ISOZYME ANALYSIS OF HEMLOCK DWARF MISTLETOE

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FINAL REPORT

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ISOZYME ANALYSES OF HEMLOCK DWARF MISTLETOE

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ABSTRACT

Three host races of hemlock dwarf mistletoe have been described: the western hemlock race (mainly parasitic on Tsuga heterophylla), the shore pine race (mainly on Pinus contorta ssp. contorta), and the mountain hemlock race (mainly on Tsuga mertensiana and Pinus monticola). Mistletoe shoots from 21 populations representing the three host races and eight host species were obtained and analyzed using starch gel electrophoresis. Over 900 individuals were examined across 13 loci. On average, 84% of the loci were polymorphic and mean heterozygosity was 0.260. The mistletoes from the Pacific Northwest (Washington, Vancouver Island, B.C., and Orcas Island) were less diverse genetically than mainland populations. Mistletoe populations parasitic on two or more hosts per population had higher numbers of alleles per locus and higher percent polymorphic loci than populations colonizing only one host.

The UPGMA phenogram showed a strong correspondence between geographic location and genetic distance indicating a clinal pattern from north to south. The most distinct cluster is composed of four populations from the Sierra Nevada in California. The population from Juneau, Alaska is also distinct but shows greater affinity to the more northern populations using UPGMA analysis. The Oregon Cascade populations referred to the mountain hemlock race were allied with the western hemlock populations with UPGMA analysis but showed affinity to the Sierra Nevada populations when analyzed with the distance Wagner procedure. Cluster and cladistic analyses did not result in discrete clusters of populations composed of either the western hemlock or shore pine races. Thus, the mountain hemlock dwarf mistletoe appears to be a separate taxon deserving of taxonomic recognition, possibly at the subspecies level. Isozyme data do not support the recognition of the shore pine race as distinct from the dwarf mistletoes on western hemlock.

INTRODUCTION

The hemlock dwarf mistletoe, Arceuthobium tsugense is an important parasite of a number of economically important conifers in the western U.S. and Canada. This mistletoe will infect 12 host species under natural conditions and at least 20 species using artificial inoculations (Smith and Craig 1968, Smith 1970, Smith and Wass 1979). Among members of the Campylopodium complex, this species exhibits the greatest host breadth.

The existence of host races (also called ecological races or pathotypes) has been suggested following field observations and inoculation trials (Smith and Wass 1976, 1979; Hunt and Smith 1978; Hawksworth and Wiens 1972, 1984). Hawksworth (1986) summarized the evidence that host races exist within this species. Table 1 summarizes the primary and secondary hosts of these races.

The distributions of the three purported host races are shown in Figure 1. The western hemlock race has a wider distribution than either the mountain hemlock or shore pine races. This form occurs from sea level to 4000 ft. in elevation and is found from a disjunct population along the coast of California in Mendocino Co. north to Juneau, Alaska. The principal hosts are western hemlock, Pacific fir, and noble fir. In mixed stands where both western and mountain hemlock occur, mountain hemlock is only rarely parasitized (Hawksworth and Wiens 1972, Shaw 1982, Mathiasen and Hawksworth 1987). The western hemlock race also rarely parasitizes Pinus monticola when these hosts occur sympatrically.

(Mathiasen 1987). Smith (1974) and Hunt and Smith (1978) attempted inoculations of western hemlock dwarf mistletoe onto western white pine in British Columbia and northern Oregon. Only rare infections or no infections were seen from these inoculations.

Several studies have focused upon the differences between the shore pine and western hemlock races (Smith 1965, 1971, 1972; Smith and Wass 1976, 1979; Wass 1976; Hunt and Smith 1978). The shore pine race occurs from sea level to 2,500 ft. from the San Juan Islands off coastal Washington to the east coast of Vancouver Island and north to the Queen Charlotte Islands. This form also occurs along coastal British Columbia from Vancouver to Terrace. The principal host is Pinus contorta ssp. contorta (shore pine). Secondary and rare hosts include Pinus monticola and Tsuga heterophylla.

Smith and Wass (1979) conducted inter-host inoculations using the seeds from both the shore pine and western hemlock races of A. tsugense. The western hemlock pathotype showed low infection (0-2%) and moderate shoot production on shore pine whereas the shore pine pathotype showed moderate infection (3-12%) but low shoot production on western hemlock. The conclusion was that this data supports the existence of host races in A. tsugense. Hawksworth and Wiens (1984) suggested that perhaps these races should be treated as "forma speciales" (special forms) as was done for A. abietinum f. sp. concoloris and A. abietinum f. sp. magnificae. To date, no consistent morphological differences have been seen between the two races (Hawksworth and Wiens 1972, Hawksworth 1986).

The mountain hemlock race occurs at high elevations (4,000 to 8,000 ft.) from the Central Cascades in Oregon to the Sierra Nevada in Central California. The principal hosts are Tsuga mertensiana (mountain hemlock) and Pinus monticola (western white pine). Secondary and rare hosts include Pinus albicaulis (whitebark pine), Abies lasiocarpa (subalpine fir), Picea engelmannii (Engelmann spruce) and P. breweriana (Brewer's spruce).

In the interest of clarifying the taxonomic status of the host races of the hemlock dwarf mistletoe, the following objectives were proposed:

1. To obtain populational samples of the three purported host races and determine genetic distance values based upon an isozyme data set.
2. To test the genetic data set to determine whether trends exist in the partitioning of variation, for example with respect to geographic location, host species, and host race.
3. To determine whether genetic variation of mistletoe populations colonizing multiple hosts differs in any way from that seen when they exist only on one host.

MATERIALS AND METHODS

Acquisition of Mistletoe Material

The locations of the 21 populations sampled for isozyme analysis are shown in Figure 2 and Table 2. Population numbers 1 through 5 were obtained during the fall of 1986. The remaining collections were made in September of 1987. These populations span the entire geographic range of the hemlock dwarf mistletoe and nearly the entire host range (8 of the 12 hosts infected in nature). The sampled populations include 7 from the western hemlock race (414 individuals), 10 from the mountain hemlock race (385 individuals), and 4 from the shore pine race (129 individuals). Population no. 7 from Horne Lake, Vancouver Island, contained dwarf mistletoes parasitic on both shore pine and western hemlock. For the purpose of the above tabulation, the mistletoes from each host species were treated as different host races. This is the only location sampled during this study where the primary host for two host races were parasitized with equal frequency.

Other populations with multiple host colonizations (nos. 2, 3, 4, 7, 11, 15, 17, 18, 19, and 20) are so indicated in Fig. 2 by symbol combinations. These represent secondary or rare host species for the particular host race as indicated in Table 1. In one population (no. 20), three host species were parasitized. In all populations with multiple host colonizations, collections of dwarf mistletoes from different hosts were given different accession numbers to allow various statistical tests of the isozyme data. When this is done, 29 populations are obtained instead of 21.

Sampling Strategy

Young dwarf mistletoe shoot clusters were clipped from host branches, placed in plastic bags, and stored cold (5 °C) until ready for enzyme extraction. Carpellate plants with maturing fruits were avoided since seed embryos and endosperms may contain different genotypes derived from one or more paternal plants. To avoid difficulty in interpreting what constituted an individual, localized infections instead of widely dispersed mistletoe shoots on broomed branches were used. Sample sizes varied but were usually greater than 20 plants per population (see Table 3). Generally no more than one carpellate and one staminate individual was taken from the same tree. Attempts were made to sample from at least 15 trees within each population.

Isozyme Methods

The extraction method and buffer reported in Nickrent (1987) was used for hemlock dwarf mistletoe tissue. Enzymes were assayed using three gel/electrode buffer systems: A) Tris-citrate pH 7.5 (Soltis et al. 1982), B) Citrate-morpholine pH 6.1 electrode, pH 6.5 gel (Nickrent 1986), and C) a Tris-Citrate, Lithium-Borate Buffer of pH 8.3 (Ridgeway et al. 1970).

Eleven enzyme systems coding for 13 putative loci were used in this study. Unless otherwise indicated, enzyme staining protocols were essentially as reported in Soltis et al. (1982). The following enzyme systems (with loci abbreviations, enzyme commission numbers, and buffer system in parentheses) were used: aconitase (ACO, E.C. 4.2.1.3, B), adenylate kinase (ADK-1, E.C. 2.7.4.3, A), alcohol dehydrogenase (ADH-1, ADH-2, E.C. 1.1.1.1, B), glucose-6-phosphate dehydrogenase (G-6-PDH, E.C. 1.1.1.49, A), glutathione reductase (Marty et al.

1984) (GSR-1, 1.6.4.2, A), isocitrate dehydrogenase (IDH, E.C. 1.1.1.42, A), malate dehydrogenase (MDH-3, MDH-4, E.C. 1.1.1.37, B), peroxidase (PER-2, E.C. 1.11.1.7, B), phosphoglucose isomerase (PGI, E.C. 5.3.1.9, A or C), phosphoglucomutase (PGM, E.C. 5.4.2.1, C), and 6-phosphogluconate dehydrogenase (6-PGDH, E.C. 1.1.1.44, B). Other enzymes such as leucine amino peptidase (LAP), fluorescent and colorimetric esterases (EST), and triose phosphate isomerase (TPI) were not consistently resolved across all populations hence they were excluded from the analysis.

Controlled crosses to document the inheritance of the isozyme patterns were not conducted, therefore genotypes inferred from the banding phenotypes should be considered putative. Banding patterns were readily interpretable since they conformed to expected patterns for monomers, dimers, etc. The plastid locus that normally stains intensely for other plants is absent or lightly staining in dwarf mistletoe. For this reason, enzyme systems such as IDH, 6-PGDH, and PGI that normally display two banding zones in diploids show only one zone on dwarf mistletoe gels.

The most common allele at a locus was assigned a mobility number of 100 and all other bands given numbers relative to it. These relative mobility numbers were then given alphabetic genotypes (AA, AB, BB) and analyzed for genetic variability using the computer program BIOSYS-1 (Swofford and Selander 1981). This program calculates allele frequencies, direct count and expected heterozygosities, F-statistics (Wright 1978, Nei 1977), genetic distances (the chord distance of Cavalli-Sforza and Edwards (1967) was used here), UPGMA cluster analysis (Sneath and Sokal 1973), hierarchical analysis of population differentiation (Wright 1978), and distance Wagner procedure (Farris 1972). For the distance Wagner procedure, the coefficient used was the chord distance of Cavalli-Sforza and Edwards (1967). Prager and Wilson's (1976) F-value was the goodness of fit criterion used for selecting partial networks saved for successive steps of the distance Wagner algorithm. A maximum of ten networks (trees) was specified to be retained for further steps of the algorithm. The tree was rooted at the midpoint of the greatest patristic length since no outgroup was included.

RESULTS

For this study, all loci examined were polymorphic in at least one population. Several loci showed large numbers of alleles such as ADH-1, IDH, MDH-3, PGM, 6-PGDH, and PER-2 (Table 3). In many instances, though, the bulk of the allelic variation was apportioned between only two alleles, such as with MDH-3¹⁰⁰ and MDH-3⁸⁰. None of the 21 populations examined showed fixation for unique alleles. Populational genetic differentiation was generally marked by differences in allele frequencies (Table 3). In general, populations from Washington, British Columbia and Alaska showed reduced genetic diversity (number of alleles) as compared with populations from the Oregon Cascades and the Sierra Nevada. This is apparent for ADH-1¹⁰⁰ which is either fixed or present at a frequency of 0.9 or greater. Conversely, the populations from the Sierra Nevada have the ADH-2⁶⁶ allele present at relatively high frequency as do those populations from the Cascades of Oregon. This contrasts with the populations from Washington and British Columbia which are fixed or nearly fixed for ADH-2¹⁰⁰. The frequencies of particular alleles at the G-6-PDH and 6-PGDH loci appear different between major geographic areas. The G-6-PDH⁹³ allele shows clinal variation with higher frequencies in the more northern populations (Washington, British Columbia) and lower frequencies in the southern populations

(Oregon Cascades, California Sierra Nevada). A similar situation exists with the 6-PGDH⁸⁹ allele. As with the ADH-2⁶⁰ allele, IDH¹²¹ is present only in the California and Oregon populations. The PGM locus showed two predominant alleles: PGM¹⁰⁰ and PGM⁷⁰. For most populations, these alleles were roughly in equal proportions, however the Mt. Findlayson population (#9) was nearly fixed for PGM⁷⁰ with a frequency of 0.917.

Genetic variability for the 21 populations across 13 loci is shown in Table 4. The mean number of alleles per locus was 2.6, the percentage of loci polymorphic was 84.2%, and the direct count of heterozygosity was 0.26. Most populations deviate little from these mean values with the exception of Mt. Findlayson and Orcas Island which were both genetically depauperate.

To determine whether a correlation exists between host latitude and genetic diversity, populations of dwarf mistletoes present on one vs. several hosts were pooled and genetic variability measures averaged. It can be seen (Table 5) that the number of alleles per locus and the percentage of polymorphic loci are higher in populations parasitizing more than one conifer host. Multiple host colonization has a geographic component, however, since the majority of populations occurring on more than one host occur in the southern portion of the range of this mistletoe species.

The partitioning of genetic variation within and between populations was examined using the Fixation Index of Wright (1978). The F_{IT} value is the fixation index of individuals relative to all populations, F_{IS} is the fixation index of individuals relative to their specific population, and F_{ST} measures the differentiation between populations relative to the limiting amount under complete fixation. An F_{ST} value of 0 indicates that all variance resides within populations. A value of 1.0 means that all of the variance is between populations, i.e. they are completely differentiated and have no alleles in common. For *Arceuthobium tsugense*, the F_{ST} value averaged across the 13 loci is 0.216 (Table 6), which indicates a moderate amount of differentiation between populations.

To analyze population differentiation hierarchically (Wright 1978), three arrangements of the populations were used. The first grouped the 22 populations shown in Table 2 according to host race (Table 7). The second method also grouped the populations according to host race but continued by dividing populations showing multiple host colonization into two or more populations; e.g. White Pass on western hemlock and White Pass on silver fir were treated as separate populations. This results in 28 total populations. The output from the hierarchical analysis provides a table giving variance components for each level of the hierarchy relative to another (Table 8). For the first two analyses, the levels are mistletoe population to total populations, mistletoe population to host race, and host race to total populations. The effect of dividing populations into two or more populations based upon host species results in little change in the variance values and no change in the overall trend. In both cases, the greater amount of the total variance is explained by the interaction between mistletoe population and host race.

The third hierarchy grouped each population (here 28 total) according to host genus and species (Table 9). As shown in Table 10, A large proportion of the variance is explained by the interaction between mistletoe population and host genus. Although less than the interaction between population and total, the comparison of population to host species also results in a high variance

component.

The chord distance measure of Cavalli-Sforza and Edwards (1967) was used to generate interpopulational genetic distance values (Table 11) and the UPGMA phenogram (Fig. 3). The phenogram shown in Fig. 3 used genetic distances between 21 populations. When populations showing multiple host colonization were divided based upon host (resulting in 28 populations as shown in Table 9), the derived sympatric populations clustered closer to each other than to any other population five of the seven possible times. This indicates that at a given site, gene flow between dwarf mistletoes on different hosts is occurring.

The phenogram in Fig. 3 also illustrates a striking correspondence between geographic location and genetic distance. The most distinct element appears as a cluster composed of populations 1-4 from the Sierra Nevada in California. These California populations, referred to mountain hemlock race, join the remaining populations at the 0.35 level. The population from Juneau, Alaska is also distinct but shows greater affinity to the remaining cluster of more northern populations. The six dwarf mistletoe populations from the Oregon Cascades, referred to the mountain hemlock race, form a discrete cluster at the 0.28 level. This cluster joins next with the Washington and British Columbia populations, not the California Sierra Nevada populations as might be expected.

Populations included within the shore pine race do not form a discrete cluster in the phenetic analysis but appear intermixed within groupings composed of the western hemlock race. The Horne Lake population is composed of individuals parasitizing both Tsuga heterophylla and Pinus contorta. This population has greatest affinity with Spider Lake which is geographically most proximal. The Mary's Peak and Mt. Findlayson populations emerge as the most dissimilar elements in the above cluster. This result stems partly from the finding that the Mt. Findlayson population shows allele frequencies for several loci that deviate from other populations.

One of the phylogenetic trees produced by the distance Wagner procedure (Farris 1972) is shown in Fig. 4. Among the four trees generated using the genetic distance of Cavalli-Sforza and Edwards (1967), this tree had the shortest total length (2.547) and the highest cophenetic correlation (0.906). As on the UPGMA phenogram, the populations assigned to the western hemlock and shore pine races are together contained within a clade distinct from the mountain hemlock race populations. The one exception involves the population from Juneau, Alaska which does not cluster with the western hemlock race populations. The distant relationship of this population to the western hemlock race is also apparent on the UPGMA phenogram. Unlike the phenetic analysis of the isozyme data, the Wagner cladogram shows a clear relationship between the mountain hemlock populations from the Cascades and those from the Sierra Nevada. The latter populations show greater affinity with two populations from Oregon: Diamond Lake (#16) and Crater Lake (#17).

DISCUSSION

In a previous study (Nickrent 1987), isozyme data were used to examine the amount and distribution of genetic variation in two closely related California taxa of Arceuthobium, A. campylopodum and A. occidentale. For these taxa, as much variance exists between the two dwarf mistletoe species categories as between any of the populations sampled, hence the recognition of one vs. two

species was appropriate. Little interpopulational genetic differentiation was seen as evidenced by an F_{ST} value of 0.093. In contrast, this study of the hemlock dwarf mistletoe indicates that a moderate amount of genetic differentiation has occurred between populations as shown by an F_{ST} value of 0.216 and the UPGMA phenogram of genetic distances.

The pattern of relationships shown in the UPGMA phenogram (Fig. 3) indicates a strong clinal trend from north to south. A similar clinal pattern resulted from isozyme analysis of three species of closed-cone pines in California (Millar et al. 1988). The relationship between the California Sierra Nevada populations of hemlock dwarf mistletoe and the Cascade populations is only clearly seen when distance Wagner trees are produced. This indicates that abrupt genetic differences between populations do not occur but instead interpopulational affinities gradually increase with decreased geographic distance.

The UPGMA phenogram and the Wagner cladogram both indicate the existence of three groups: the western hemlock/shore pine populations, the Cascade Range populations from Oregon, and the Sierra Nevada populations. The distinctiveness of the western hemlock/shore pine group is in agreement with field observations and inoculation trials (Hawksworth and Wiens 1972, Smith and Wass 1976, Hunt and Smith 1978, Shaw 1982). Stands where western hemlock and western white pine occur together are relatively rare and unfortunately none of the sites sampled for this isozyme study included both these hosts. Mathiasen and Hawksworth (1987) reported infection percentages for these two hosts at five sites near Union Creek, Douglas Co., Oregon, however specific locality information was lacking. In that study, infection of *P. monticola* in *T. heterophylla* stands was rare. Unfortunately, no population of dwarf mistletoe on western hemlock was obtained from this area for isozyme analysis. One population located 15 miles NE of Union Creek (Beaver Meadow, #19) was used for this isozyme study and showed heavy infestation of both mountain hemlock and western white pine. This indicates that within very short distances, infection characteristics vary widely among host species. If the western and mountain hemlock races are indeed sympatric near Union Creek, populations from this area should be subjected to further sampling for isozyme analyses.

The electrophoretic evidence does not at present indicate a comparable level of genetic differentiation between the western hemlock and purported shore pine races as was seen with the mountain hemlock race. Two of the four populations referred to the shore pine race (Spider Lake and Horne Lake) cluster together in the UPGMA phenogram, whereas the other two (Mt. Findlayson and Orcas Island) do not. Upon distance Wagner analysis, however, the four shore pine populations do form a distinct clade. This clade, however, is contained within other populations of the western hemlock race, hence the group is polyphyletic. Given that both shore pine and western hemlock were both heavily infected at the Horne Lake population, and the high level of genetic similarity among mistletoes from the two hosts, it appears that these plants are not reproductively isolated. The recognition of two host races at this location would be artificial and misleading and would not serve to describe genetically differentiated biological units.

As shown in Table 4, the Mt. Findlayson and Orcas Island populations are genetically depauperate compared with the mean values for all populations. These populations are geographically isolated from other populations which may result in restricted gene flow. The low genetic diversity seen for these

populations may be the result of a founder event (a small number of genetically "atypical" seeds colonizing the site) or the extreme truncation of a formerly more widespread population (a population crash). In either case, random genetic drift in the small population can result in fixation for alternate alleles and reduction of the population's overall genetic diversity as was observed for these two populations.

Since the western hemlock and shore pine pathotypes were the subject of the artificial inoculation trials by Smith and Wass (1979), a review of their findings is in order. Table 12 summarizes the results of that study and indicates the percent germination, percent infection, swelling dimensions, and shoot number and shoot heights. Seeds from each dwarf mistletoe pathotype result in more infections on the primary host than on the alternate host. Seeds derived from the shore pine race, however, resulted in 12 and 3% infection on western hemlock for 1970 and 1971 respectively. Shoot production following infection was low, however, for this host/parasite combination. These results indicate that the shore pine race is more "aggressive", even on an alternate host, than is the western hemlock race. This is also shown by the significantly higher infection percentages obtained on its primary host (39, 58%). The 12% infection rate for shore pine pathotype seeds on western hemlock in 1970 is nearly as high as the percent infection of western hemlock pathotype seeds placed on western hemlock in 1971 (13%). The seed source for the shore pine pathotype of A. tsugense was collected at Horne Lake, Vancouver Island. This is the same locality as population number 7 in this study. As already noted, both shore pine and western hemlock are naturally parasitized at this site. This fact was not mentioned by Smith and Wass (1979) but is relevant given the given the relatively high rate of infection on western hemlock in 1970.

Since no morphological differences are apparent between the shore pine and western hemlock pathotypes of A. tsugense, inoculation studies (Smith and Wass 1976, 1979; Hunt and Smith 1978) remain the primary evidence supporting their recognition. Although these studies provide valuable information, they remain limited for several reasons. First it is difficult to establish the proper controls when conducting artificial inoculation studies with dwarf mistletoe seeds. Infection success varies widely as has been reported for inoculations of both primary and secondary host species (Parmeter and Scharpf 1963, Scharpf and Parmeter 1967, Hawksworth et al. 1985). Second, the biological and ecological significance of these types of studies are questionable because of the frequent small number of samples and sites used. For example, Smith and Wass (1979) do not mention how many dwarf mistletoe individuals were used as seed sources. In addition, only one population each of the shore pine pathotype (Horne Lake) and western hemlock pathotype (Cowichan Lake) was used. Projects involving additional accessions of dwarf mistletoe seeds collected throughout the range of the taxon and then inoculated onto hosts at several sites would make such studies more meaningful.

Information on the genetic makeup of the host and parasite populations as well individual genotypes of plants being used for experimentation would be valuable. Sampling from the entire range of the taxon has already been mentioned. This will present a more representative picture of the range of genetic variability of the mistletoe. Since electrophoretic studies have shown that members of the Campylopodium complex, including A. tsugense, are variable at most isozyme loci examined, it is reasonable to assume that the genes responsible for host pathogenicity also exist with multiple alleles. This assumes that the variation measured by electrophoretic means provides some

indication of the total genetic variation, including those genes responsible for host parasitism. Evidence that electrophoretically characterized genetic variation and host latitude are at least loosely correlated is shown in this study where A. tsugense populations colonizing more than one host are genetically more variable than populations colonizing a single host. This correlation could be further tested by choosing electrophoretically variable and monomorphic populations and using these seeds for inoculation trials on several different host species.

It is likely that in addition to host specificity at the "taxonomic level" (i.e. host genera, host species), that dwarf mistletoes are also adapted to particular ecological zones inhabited by the host species. As is known in California for Douglas fir, tree seed zones (National Council on Gene Resources 1982) exist based upon climate, topography and soil conditions. These zones are used to reduce the risks associated with planting seeds in nonoptimal sites. The mosaic pattern of these zones may also be interpreted as zones of genetic variation for this tree species. If similar zones also exist within a particular dwarf mistletoe species, the zones may or may not coincide exactly with the zones of one or more host species.

The results of this study indicate a higher level of genetic differentiation between A. tsugense populations than was seen for A. campylopodum and A. occidentale. For the western hemlock and the mountain hemlock races, documented host preference differences and now genetic differences visualized from isozymes, raise a question concerning the correct placement of these taxa within the taxonomic hierarchy. To test the validity of these host races using the biological species concept requires information on reproductive isolation. Direct (experimental) evidence involving crossing experiments is unfortunately lacking for these host races. The isozyme data reported here do not indicate strong isolating barriers but show a continuum of genetic distance values, albeit with some indication of a break between the mountain hemlock race and the remaining populations. The intermediate status of the Cascade populations does not indicate genetic isolation but that gene flow is occurring. The western hemlock and mountain hemlock dwarf mistletoes are, for the most part, allopatric based upon host preference and the ranges of their principal host species. For populations that are morphologically identical, not reproductively isolated, and allopatric, the taxonomic rank of subspecies was suggested by Mayr (1948, 1982). For the dwarf mistletoes, the rank of forma speciales also has been used for A. abietinum. In the case of the fir dwarf mistletoe, however, there does not appear to be a correlation with geographic location and genetic differentiation as seen with A. tsugense (Nickrent 1986).

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Table 1. Natural Hosts for Three Host Races of Arceuthobium tsugense.

Race	Primary Hosts	Secondary and Rare Hosts
I. Western Hemlock	<u>Tsuga heterophylla</u> <u>Abies amabilis</u> <u>Abies procera</u>	<u>Tsuga mertensiana</u> <u>Pinus monticola</u> <u>Picea sitchensis</u>
II. Mountain Hemlock	<u>Tsuga mertensiana</u> <u>Pinus monticola</u>	<u>Pinus albicaulis</u> <u>Abies lasiocarpa</u> <u>Abies grandis</u> <u>Picea engelmannii</u> <u>Picea breweriana</u>
III. Shore Pine	<u>Pinus contorta</u> ssp. <u>contorta</u>	<u>Tsuga heterophylla</u> <u>Pinus monticola</u>

Table 2. Hemlock Dwarf Mistletoe Collections Used in Isozyme Study

Pop. No.	Name/Location	Host Race ¹	Hosts
1.	Lassen N. P., Cal.	MH	<u>Tsuga mertensiana</u>
2.	Silver Lake, Cal.	MH	<u>T. mertensiana</u> , <u>Pinus monticola</u>
3.	Alpine Meadow, Cal.	MH	<u>T. mertensiana</u> , <u>P. monticola</u>
4.	Mosquito Lake, Cal.	MH	<u>T. mertensiana</u> , <u>P. monticola</u>
5.	Juneau, Alaska	WH	<u>T. heterophylla</u>
6.	Cowichan, B.C.	WH	<u>T. heterophylla</u>
7.	Horne Lake, B.C.	WH/SP	<u>T. heterophylla</u> , <u>P. contorta</u>
8.	Spider Lake, B.C.	SP	<u>P. contorta</u>
9.	Mt. Findlayson, B.C.	SP	<u>P. contorta</u>
10.	Nemah, Wash.	WH	<u>T. heterophylla</u>
11.	White Pass, Wash.	WH	<u>T. heterophylla</u> , <u>Abies amabilis</u>
12.	Silver Creek, Wash.	WH	<u>T. heterophylla</u>
13.	Huckleberry, Wash.	WH	<u>T. heterophylla</u>
14.	Mary's Pk., Oreg.	WH	<u>Abies procera</u>
15.	Windigo Pass, Oreg.	MH	<u>T. mertensiana</u> , <u>P. monticola</u>
16.	Diamond Lk., Oreg.	MH	<u>T. mertensiana</u>
17.	Crater Lk., Oreg.	MH	<u>P. albicaulis</u> , <u>T. mertensiana</u>
18.	1000 Springs, Oreg.	MH	<u>T. mertensiana</u> , <u>A. lasiocarpa</u>
19.	Beaver Mdw., Oreg.	MH	<u>P. monticola</u> , <u>T. mertensiana</u>
20.	McKenzie Pass, Oreg.	MH	<u>T. mertensiana</u> , <u>A. lasiocarpa</u> , <u>P. albicaulis</u>
21.	Orcas Island, B.C.	SP	<u>P. contorta</u>

¹ MH = Mt. Hemlock, WH = Western Hemlock, and SP = Shore Pine Race

Table 3. Allele frequencies for 21 populations of *Arceuthobium tsugense*

Locus	Population																				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
ACO-1																					
(N)	14	30	46	18	17	41	91	52	24	20	82	45	63	31	27	24	32	26	46	48	26
105	.071	.033	.033	.139	.029	.024	.005	.000	.000	.050	.043	.000	.000	.129	.019	.125	.359	.000	.022	.094	.019
100	.500	.567	.543	.306	.971	.902	.995	1.000	1.000	.900	.671	.911	.960	.645	.926	.750	.578	.904	.891	.667	.981
92	.429	.183	.315	.500	.000	.024	.000	.000	.000	.050	.280	.089	.040	.113	.056	.042	.000	.096	.087	.240	.000
95	.000	.133	.065	.056	.000	.024	.000	.000	.000	.000	.000	.000	.000	.000	.000	.083	.063	.000	.000	.000	.000
89	.000	.083	.043	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.113	.000	.000	.000	.000	.000	.000	.000
85	.000	.000	.000	.000	.000	.024	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
80	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.006	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
ADH-1																					
(N)	18	39	69	40	24	41	91	52	24	39	89	46	64	32	31	28	32	27	47	51	33
133	.000	.000	.000	.013	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
125	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.011	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
120	.000	.000	.000	.112	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
115	.028	.000	.000	.025	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.016	.000	.032	.000	.000
112	.000	.000	.036	.000	.000	.000	.000	.000	.000	.064	.028	.000	.047	.000	.016	.179	.031	.074	.011	.108	.000
100	.972	1.000	.964	.850	1.000	1.000	1.000	1.000	1.000	.936	.961	1.000	.953	1.000	.984	.821	.922	.926	.926	.863	1.000
71	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.032	.000	.000
65	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.031	.000	.000	.000	.000
82	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.029	.000
ADH-2																					
(N)	18	39	69	35	24	41	90	52	24	39	89	46	64	32	26	27	32	27	48	50	33
100	.917	.462	.971	.843	1.000	1.000	.989	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.577	.889	.609	.815	.688	.580	1.000
78	.000	.000	.014	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.010	.000	.000
66	.083	.538	.014	.157	.000	.000	.011	.000	.000	.000	.000	.000	.000	.000	.423	.111	.391	.185	.302	.420	.000
45	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
ADK																					
(N)	18	37	69	39	24	38	90	48	24	40	89	46	64	32	30	28	32	27	46	51	29
121	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.022	.000	.000
109	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.008	.000	.000	.000	.000	.000	.000	.000	.000
100	.972	1.000	1.000	1.000	1.000	.908	.989	1.000	1.000	.925	.983	1.000	.953	.953	.983	1.000	.984	1.000	.946	.882	1.000
92	.028	.000	.000	.000	.000	.092	.011	.000	.000	.075	.017	.000	.039	.047	.000	.000	.016	.000	.033	.118	.000
78	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.017	.000	.000	.000	.000	.000	.000

Table 3, con.

Locus	Population																				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
QSR																					
(N)	13	40	69	38	24	25	90	42	24	39	87	46	61	32	29	27	30	24	45	48	33
109	.115	.000	.000	.066	.000	.000	.000	.000	.000	.000	.011	.011	.000	.000	.000	.019	.000	.000	.000	.000	.000
105	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.103	.093	.050	.042	.000	.042	.030
100	.885	1.000	1.000	.895	.958	.780	.328	.452	.979	.641	.586	.565	.623	.563	.828	.889	.550	.917	1.000	.646	.788
93	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.016	.000	.000	.000	.000	.000	.000	.000	.000
86	.000	.000	.000	.039	.042	.220	.672	.548	.021	.359	.402	.402	.361	.438	.069	.000	.400	.042	.000	.313	.182
75	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.022	.000	.000	.000	.000	.000	.000	.000	.000	.000
Q-6PDH																					
(N)	18	40	67	32	23	41	90	52	24	29	85	41	62	27	28	24	29	22	43	49	33
106	.000	.000	.000	.031	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
100	.861	.975	1.000	.953	.457	.415	.583	.471	.063	.741	.400	.524	.427	.907	.643	.875	.931	.909	.674	.918	.242
93	.083	.025	.000	.016	.543	.573	.411	.529	.938	.259	.553	.476	.573	.074	.321	.125	.000	.000	.326	.061	.742
82	.056	.000	.000	.000	.000	.012	.006	.000	.000	.000	.000	.000	.000	.019	.036	.000	.000	.000	.000	.020	.015
76	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.047	.000	.000	.000	.000	.000	.069	.091	.000	.000	.000
IDH																					
(N)	18	39	69	40	24	31	91	50	24	40	89	46	64	32	30	28	32	27	47	51	33
142	.111	.000	.000	.013	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
135	.028	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
127	.000	.000	.000	.013	.000	.000	.203	.340	.021	.013	.090	.239	.070	.250	.083	.018	.219	.000	.149	.088	.000
121	.417	.218	.703	.112	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.033	.054	.000	.056	.043	.078	.000
115	.000	.000	.000	.038	.000	.000	.005	.020	.000	.000	.006	.011	.000	.016	.000	.000	.000	.000	.011	.010	.000
100	.444	.782	.297	.825	1.000	1.000	.791	.640	.979	.962	.904	.750	.930	.734	.883	.929	.781	.944	.755	.824	1.000
89	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.032	.000	.000
78	.000	.000	.000	.000	.000	.000	.000	.000	.000	.025	.000	.000	.000	.000	.000	.000	.000	.000	.011	.000	.000
MDH-3																					
(N)	18	40	68	40	24	41	91	52	24	40	89	45	63	32	31	28	32	27	48	50	33
123	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.010	.000
117	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.016	.000	.000	.000	.000	.000	.000
109	.000	.000	.007	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
104	.000	.000	.007	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
100	.667	.762	.382	.837	.771	.671	.753	.712	.792	.587	.618	.733	.786	.688	.581	.804	.578	.741	.865	.480	.561
95	.028	.000	.029	.000	.000	.000	.000	.000	.000	.000	.006	.022	.000	.000	.000	.000	.000	.000	.000	.000	.091
86	.000	.000	.022	.000	.000	.000	.000	.000	.000	.025	.028	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
83	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.015
80	.194	.213	.551	.162	.229	.329	.247	.288	.208	.387	.348	.244	.206	.313	.387	.196	.422	.259	.135	.500	.333
75	.028	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.008	.000	.000	.000	.000	.000	.000	.010	.000
60	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.016	.000	.000	.000	.000	.000	.000
54	.000	.025	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
45	.083	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000

-16-

Ent.

	Population																				
Locus	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
MDH-4																					
(N)	16	39	68	39	12	41	90	52	24	40	89	46	64	32	31	27	32	27	48	51	33
100	.969	.654	.662	1.000	.500	.927	.961	1.000	1.000	.938	.955	.989	1.000	.906	.887	.741	.578	.778	.698	.833	1.000
56	.000	.167	.000	.000	.000	.024	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.020	.000
32	.000	.179	.338	.000	.000	.000	.000	.000	.000	.013	.006	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
-20	.031	.000	.000	.000	.500	.049	.039	.000	.000	.050	.039	.011	.000	.094	.113	.259	.422	.222	.229	.147	.000
-31	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.073	.000	.000
PGI																					
(N)	18	40	68	40	24	36	91	45	24	39	88	45	64	32	31	28	31	27	48	51	33
150	.000	.000	.000	.000	.000	.014	.000	.000	.000	.000	.000	.000	.016	.000	.000	.000	.000	.000	.000	.000	.000
133	.444	.363	.191	.175	.021	.153	.060	.011	.271	.244	.102	.189	.273	.016	.161	.393	.194	.130	.208	.118	.136
100	.556	.637	.809	.825	.979	.778	.940	.989	.729	.756	.898	.789	.711	.984	.839	.607	.806	.870	.792	.882	.864
70	.000	.000	.000	.000	.000	.056	.000	.000	.000	.000	.000	.022	.000	.000	.000	.000	.000	.000	.000	.000	.000
PGM																					
(N)	18	40	69	40	24	41	91	49	24	35	88	46	64	32	31	28	32	26	48	51	33
111	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.011	.000	.000	.000	.000	.000	.000	.021	.000	.000
100	.833	.450	.565	.463	.542	.463	.582	.551	.083	.571	.659	.772	.602	.188	.839	.464	.344	.635	.760	.657	.424
85	.028	.000	.101	.025	.000	.012	.027	.010	.000	.000	.011	.000	.000	.000	.000	.000	.000	.154	.000	.000	.000
80	.000	.000	.022	.013	.000	.000	.005	.000	.000	.043	.000	.000	.008	.000	.000	.000	.000	.000	.000	.010	.000
70	.139	.550	.312	.500	.438	.524	.385	.439	.917	.386	.330	.217	.391	.813	.161	.536	.656	.212	.219	.333	.576
65	.000	.000	.000	.000	.021	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
6-PGDH																					
(N)	18	40	69	40	24	41	90	52	24	40	88	46	62	32	29	27	32	26	48	50	33
142	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.016	.000	.000	.000	.000	.000	.000	.000	.000
132	.278	.363	.000	.188	.000	.146	.011	.000	.000	.075	.045	.000	.040	.000	.000	.278	.047	.000	.000	.060	.000
123	.083	.000	.000	.000	.000	.037	.000	.000	.000	.025	.000	.011	.032	.047	.000	.204	.016	.019	.073	.040	.000

Table 3, cont.

Locus	Population																				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
PER-2																					
(N)	5	21	65	38	12	39	90	51	23	39	80	46	55	32	29	28	32	25	44	50	24
104	.000	.000	.000	.026	.000	.000	.000	.000	.000	.013	.006	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
100	.500	.476	.700	.513	.375	.397	.489	.686	.674	.487	.456	.304	.164	.266	.328	.518	.531	.140	.364	.210	.458
97	.000	.143	.069	.066	.083	.115	.000	.010	.326	.231	.050	.087	.018	.125	.121	.000	.000	.640	.136	.350	.021
92	.300	.381	.023	.303	.000	.179	.094	.098	.000	.013	.081	.370	.464	.094	.034	.054	.078	.020	.057	.100	.417
88	.000	.000	.000	.026	.000	.000	.000	.000	.000	.205	.250	.000	.255	.516	.034	.000	.016	.180	.159	.260	.000
86	.100	.000	.008	.026	.542	.167	.044	.088	.000	.026	.031	.000	.018	.000	.293	.429	.375	.020	.000	.000	.021
80	.000	.000	.062	.039	.000	.141	.194	.059	.000	.026	.119	.239	.082	.000	.190	.000	.000	.000	.273	.070	.083
75	.100	.000	.123	.000	.000	.000	.000	.000	.000	.000	.006	.000	.000	.000	.000	.000	.000	.000	.011	.010	.000
72	.000	.000	.000	.000	.000	.000	.039	.059	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
63	.000	.000	.008	.000	.000	.000	.100	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
59	.000	.000	.008	.000	.000	.000	.022	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
54	.000	.000	.000	.000	.000	.000	.017	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000

Table 4. Genetic variability at 13 loci in 21 populations of *A. tsugense*

Population	Mean sample size per Locus	Mean no. of alleles per locus	Percentage of loci polymorphic ¹	Mean heterozygosity	
				Direct- count	HdyWbg expected ²
1. Hemlock Lake	16.2	3.1	100.0	.267	.367
2. Mt. Elwell	37.2	2.3	76.9	.258	.352
3. Alpine Meadow	66.5	3.1	76.9	.253	.293
4. Mosquito Lake	36.8	3.2	84.6	.264	.302
5. Juneau	21.5	1.8	69.2	.204	.234
6. Cowichan	38.2	2.9	76.9	.270	.315
7. Horne Lake	90.5	2.8	92.3	.230	.253
8. Spider Lake	49.9	2.1	61.5	.236	.238
9. Mt. Findlayson	23.9	1.6	61.5	.094	.125
10. Nemah	36.8	2.9	92.3	.292	.317
11. White Pass	87.1	3.2	92.3	.285	.313
12. Silver Creek	45.4	2.4	76.9	.274	.265
13. Huckleberry	62.6	2.8	84.6	.250	.292
14. Mary's Peak	31.5	2.4	84.6	.296	.280
15. Windigo Pass	29.5	2.8	100.0	.246	.326
16. Diamond Lake	27.1	2.5	92.3	.339	.346
17. Crater Lake	31.5	2.6	100.0	.327	.394
18. 1000 Springs	26.0	2.4	92.3	.249	.280
19. Beaver Meadows	46.6	3.2	92.3	.298	.343
20. McKenzie Pass	50.1	3.3	100.0	.362	.394
21. Orcas Island	31.5	2.2	61.5	.185	.211
Means	42.2	2.6	84.2	.260	.297

¹ A locus is considered polymorphic if more than one allele was detected
² Unbiased estimate (see Nei, 1978)

Table 5. Genetic Diversity for Hemlock Dwarf Mistletoe Populations
Colonizing Different Numbers of Host Species

	# Pops.	Mean Sample Size	Mean # Alleles/ Locus	% Loci Poly- morphic ¹	Mean Heterozygosity	
					Direct Count	HdyWbg Expected ²
Populations on 2 or more hosts	10	50.1	2.89	90.7	0.277	0.325
Populations on one host	11	34.9	2.42	78.3	0.246	0.271
All Populations	21	42.2	2.60	84.2	0.260	0.297

¹ A locus is considered polymorphic if more than one allele was detected

² Unbiased estimate (Nei 1978)

Table 6. Summary of F-statistics at 13 Loci
for Arceuthobium tsugense

Locus	F_{IS}	F_{IT}	F_{ST}
ACO-1	.206	.366	.202
ADH-1	.082	.154	.079
ADH-2	-.012	.318	.326
ADK-1	.217	.260	.054
GSR-1	-.039	.217	.246
G6PDH	.196	.447	.312
IDH-1	.018	.259	.245
MDH-3	-.133	-.033	.088
MDH-4	.221	.405	.236
PGI-1	.081	.181	.108
PGM-1	.034	.169	.141
6PGDH	.080	.385	.331
PER-2	.228	.383	.201
Mean	.086	.283	.216

Table 7. Hierarchical Levels for 22 Populations Grouped by Host Race

1. **WESTERN HEMLOCK**

Juneau	WH
Cowichan	WH
Horne Lake	WH *
Nemah	WH
White Pass	WH/SLF
Silver Creek	WH
Huckleberry	WH
Mary's Peak	NBF

2. **MT. HEMLOCK**

Hemlock Lake	MH
Mt. Elwell	MH/WWP
Alpine Meadow	MH/WWP
Mosquito Lake	MH/WWP
Windigo Pass	MH/WWP
Diamond Lake	MH
Crater Lake	MH/WBP
1000 Springs	MH
Beaver Meadows	MH/WWP
McKenzie Pass	MH/WBP/SAF

3. **SHORE PINE**

Horne Lake	SP *
Spider Lake	SP
Mt. Findlayson	SP
Orcas Island	SP

* Horne Lake is actually one population, split here according to host race

Table 8. Variance Components and F-statistics Combined Across Loci¹

Comparison		22 Populations; Defined by Host Race		28 Populations; Defined by Host Race	
X	Y	Variance Component	F _{XY}	Variance component	F _{XY}
Population	Total	.87888	.187	.94739	.197
Population	Host Race	.64659	.145	.72703	.159
Host Race	Total	.23229	.049	.22036	.046

¹ Sympatric dwarf mistletoes occurring on different hosts defined as same population (giving 22 total) or different populations (28 total).

Table 9. Hierarchical Levels for 28 Populations Grouped by Host Genus and Species

1. Tsuga
 1. heterophylla
 - Juneau
 - Cowichan
 - Horne Lake
 - Nemah
 - White Pass
 - Silver Creek
 - Huckleberry
 2. mertensiana
 - Hemlock Lake
 - Mt. Elwell
 - Alpine Meadow
 - Mosquito Lake
 - Windigo Pass
 - Diamond Lake
 - 1000 Springs
 - Beaver Meadows
 - McKenzie Pass
2. Pinus
 1. albicaulis
 - Crater Lake
 - McKenzie Pass
 2. contorta
 - Horne Lake
 - Spider Lake
 - Mt. Findlayson
 - Orcas Island
 3. monticola
 - Mt. Elwell
 - Alpine Meadow
 - Beaver Meadow
3. Abies
 1. amabilis
 - White Pass
 2. lasiocarpa
 - McKenzie Pass
 3. procera
 - Mary's Peak

Table 10. Variance Components and F-statistics Combined Across Loci 28
Populations Defined by Host Species and Locality

Comparison		Variance component	F _{XY}
X	Y		
Population	Host Genus	1.11131	.224
Population	Total	.94744	.197
Population	Host Species	.71308	.156
Host Species	Host Genus	.39823	.080
Host Species	Total	.23436	.049
Host Genus	Total	-.16387	-.034

Table 11. Matrix of Genetic Distance Coefficients for *Arceuthobium tsugense*¹

Population	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
1 Hemlock Lake, CA	***	.271	.276	.228	.359	.306	.370	.381	.411	.322	.327	.358	.331	.378	.311	.261	.347	.325	.302	.319	.368
2 Mt. Elwell, CA	.182	***	.270	.215	.378	.313	.385	.393	.387	.327	.355	.379	.346	.367	.313	.283	.327	.302	.302	.299	.376
3 Alpine Meadow, CA	.189	.209	***	.269	.373	.347	.383	.384	.407	.324	.345	.389	.378	.373	.328	.332	.367	.300	.320	.333	.396
4 Mosquito Lake, CA	.156	.147	.195	***	.344	.286	.343	.350	.384	.288	.291	.343	.307	.317	.294	.272	.299	.283	.277	.280	.359
5 Juneau, AK	.282	.257	.267	.235	***	.261	.332	.326	.337	.291	.322	.374	.337	.358	.285	.287	.312	.311	.306	.371	.346
6 Cowichan, B.C.	.234	.237	.273	.211	.155	***	.206	.216	.244	.177	.191	.219	.183	.268	.228	.246	.293	.291	.260	.266	.198
7 Horne Lake, B.C.	.272	.301	.308	.261	.216	.143	***	.111	.280	.218	.192	.171	.202	.251	.243	.314	.294	.332	.289	.283	.206
8 Spider Lake, B.C.	.282	.314	.304	.271	.209	.142	.061	***	.249	.228	.193	.170	.207	.247	.252	.324	.312	.341	.302	.305	.194
9 Mt. Findlayson, B.C.	.320	.301	.344	.285	.234	.162	.197	.182	***	.259	.268	.270	.272	.309	.308	.337	.394	.347	.321	.355	.206
10 Nemah, WA	.224	.251	.245	.218	.212	.097	.135	.151	.195	***	.149	.232	.178	.202	.228	.260	.278	.239	.242	.200	.244
11 White Pass, WA	.236	.285	.266	.233	.215	.116	.110	.115	.200	.102	***	.185	.160	.208	.227	.294	.303	.280	.250	.225	.217
12 Silver Creek, WA	.236	.289	.306	.255	.238	.137	.091	.099	.191	.137	.107	***	.182	.262	.255	.333	.356	.332	.278	.277	.174
13 Huokleberry, WA	.244	.267	.312	.235	.199	.100	.126	.132	.172	.098	.100	.100	***	.232	.249	.295	.326	.299	.255	.252	.200
14 Mary's Peak, OR	.271	.270	.293	.243	.275	.187	.157	.158	.232	.153	.145	.172	.184	***	.294	.326	.285	.282	.288	.224	.288
15 Windigo Pass, OR	.221	.227	.268	.233	.209	.146	.179	.204	.247	.138	.159	.162	.173	.230	***	.244	.256	.231	.196	.209	.266
16 Diamond Lake, OR	.189	.172	.255	.174	.190	.173	.239	.254	.243	.176	.230	.245	.206	.230	.195	***	.227	.285	.274	.287	.315
17 Crater Lake, OR	.269	.207	.252	.214	.240	.227	.249	.257	.330	.204	.235	.261	.261	.197	.195	.183	***	.292	.302	.267	.357
18 1000 Springs, OR	.221	.207	.227	.181	.192	.190	.230	.257	.263	.166	.212	.218	.206	.225	.152	.164	.204	***	.236	.215	.351
19 Beaver Meadows, OR	.207	.196	.237	.195	.192	.183	.207	.239	.257	.173	.203	.181	.190	.250	.121	.180	.200	.130	***	.225	.316
20 McKenzie Pass, OR	.248	.223	.254	.224	.295	.200	.214	.238	.314	.138	.153	.209	.195	.169	.140	.215	.178	.162	.187	***	.317
21 Orcas Island, WA	.283	.281	.315	.247	.206	.097	.142	.130	.117	.152	.130	.122	.124	.206	.189	.233	.279	.239	.247	.242	*****

¹ Above diagonal: Cavalli-Sforza and Edwards (1967) chord distance

Below diagonal: Rogers (1972) genetic distance

Table 12. Summary of Results of the A. tsugense Pathotype Cross Inoculation Study by Smith and Wass (1979)¹

Dwarf Mistletoe & Source Host	HOSTS									
	Western Hemlock (WH) Victoria, B.C.					Shore Pine (SP) Victoria, B.C.				
	Germ. %	Infect. %	Swell. Length (mm)	#	Shoot Height (mm)	Germ. %	Infect. %	Swell. Length (mm)	#	Shoot Height (mm)
TSU-WH Cowichan B.C.	47 ²	20	75 ³	18	37	52	0	35	5	43
	39	13				79	2			
TSU-SP Horne Lk. B.C.	74	12	19	0.2	2	82	39	45	16	37
	61	3				85	58			

¹ Percentages based upon 300 seeds in each mistletoe/host/location combination

² Top figure for 1970, bottom for 1971

³ Averaged for both years

Figure Legends

1. Distribution of Arceuthobium tsugense. The solid outline encloses the range of the western hemlock race, the dots the mountain hemlock race, and the small stipple the shore pine race.
2. Locations of the hemlock mistletoe populations collected for isozyme analysis. Symbols indicate host or hosts parasitized at each site. For multiple host colonizations, the symbols are used in combination. MH = mountain hemlock (Tsuga mertensiana), WH = western hemlock (Tsuga heterophylla), SP = shore pine (Pinus contorta ssp. contorta), WBP = white bark pine (Pinus albicaulis), WWP = western white pine (Pinus monticola), NBF = noble fir (Abies procera), SLF = silver fir (Abies amabilis), and SAF = subalpine fir (Abies lasiocarpa).
3. UPGMA phenogram using the chord distance of Cavalli-Sforza and Edwards (1967) for 21 populations of hemlock dwarf mistletoe listed in Table 2. WH = western hemlock race, SP = shore pine race, and MH = mountain hemlock race.
4. Distance Wagner cladogram using chord distance of Cavalli-Sforza and Edwards (1967). WH = western hemlock race, SP = shore pine race, and MH = mountain hemlock race.

Figure 1.

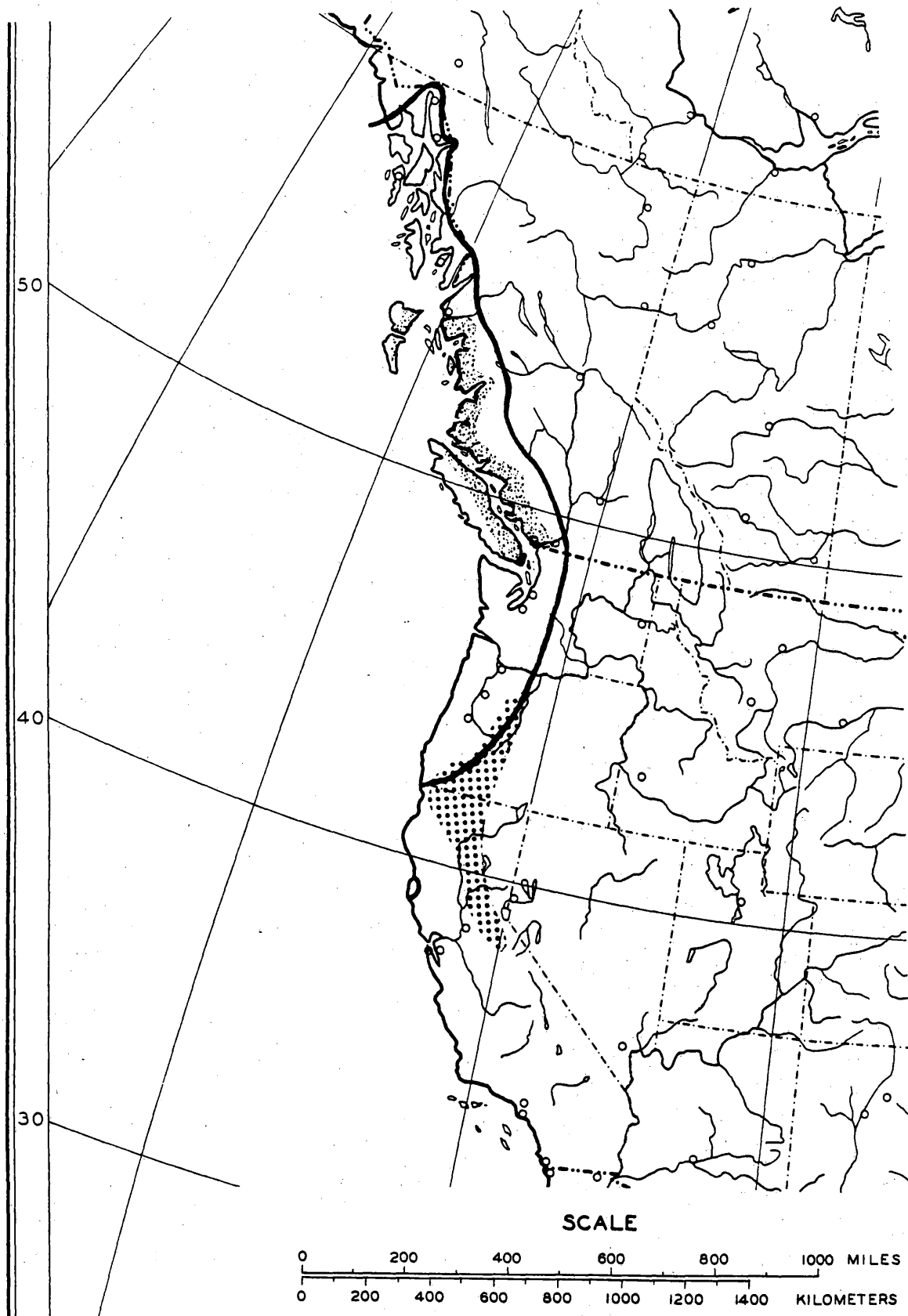


Figure 2

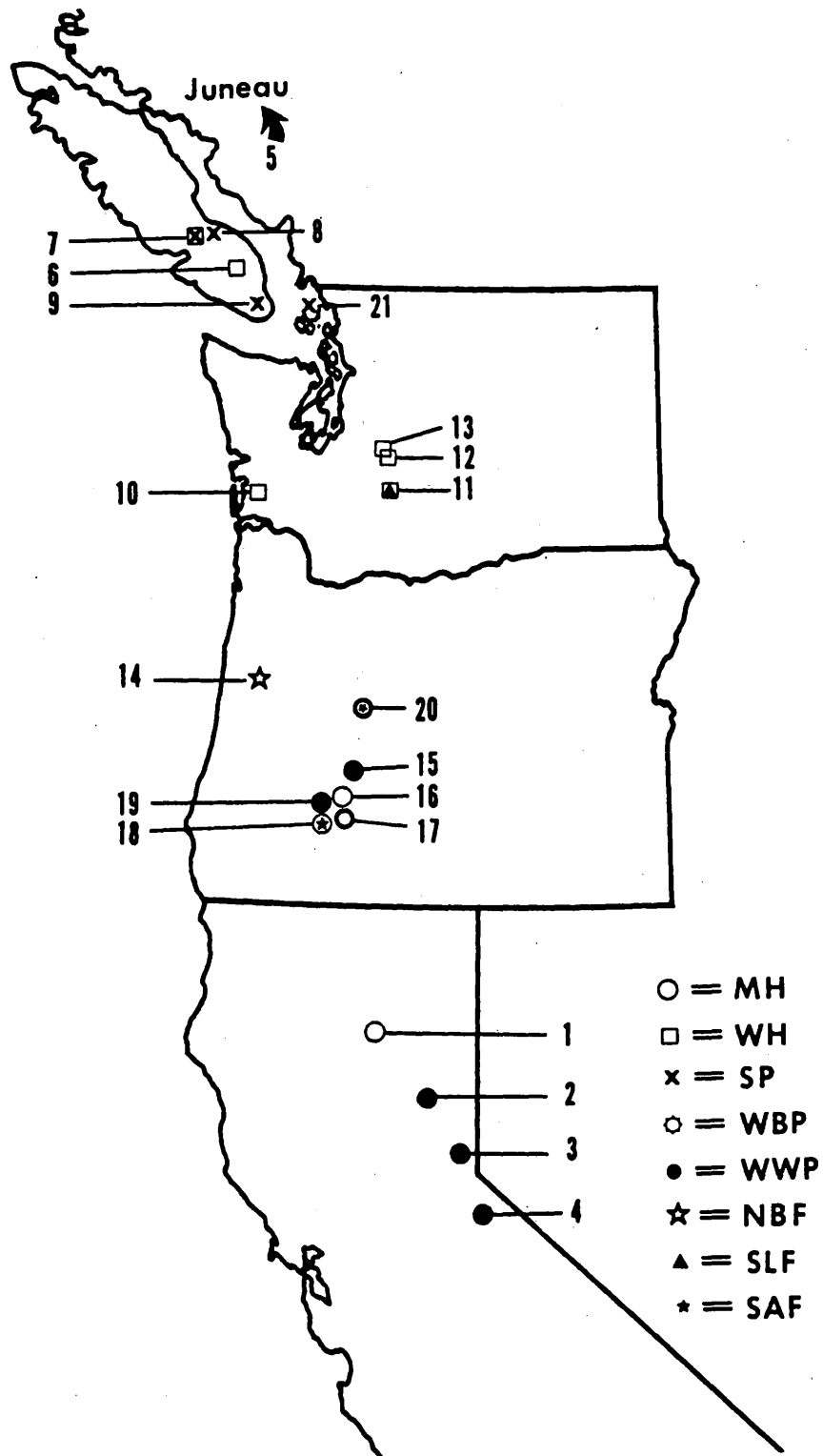


Figure 3

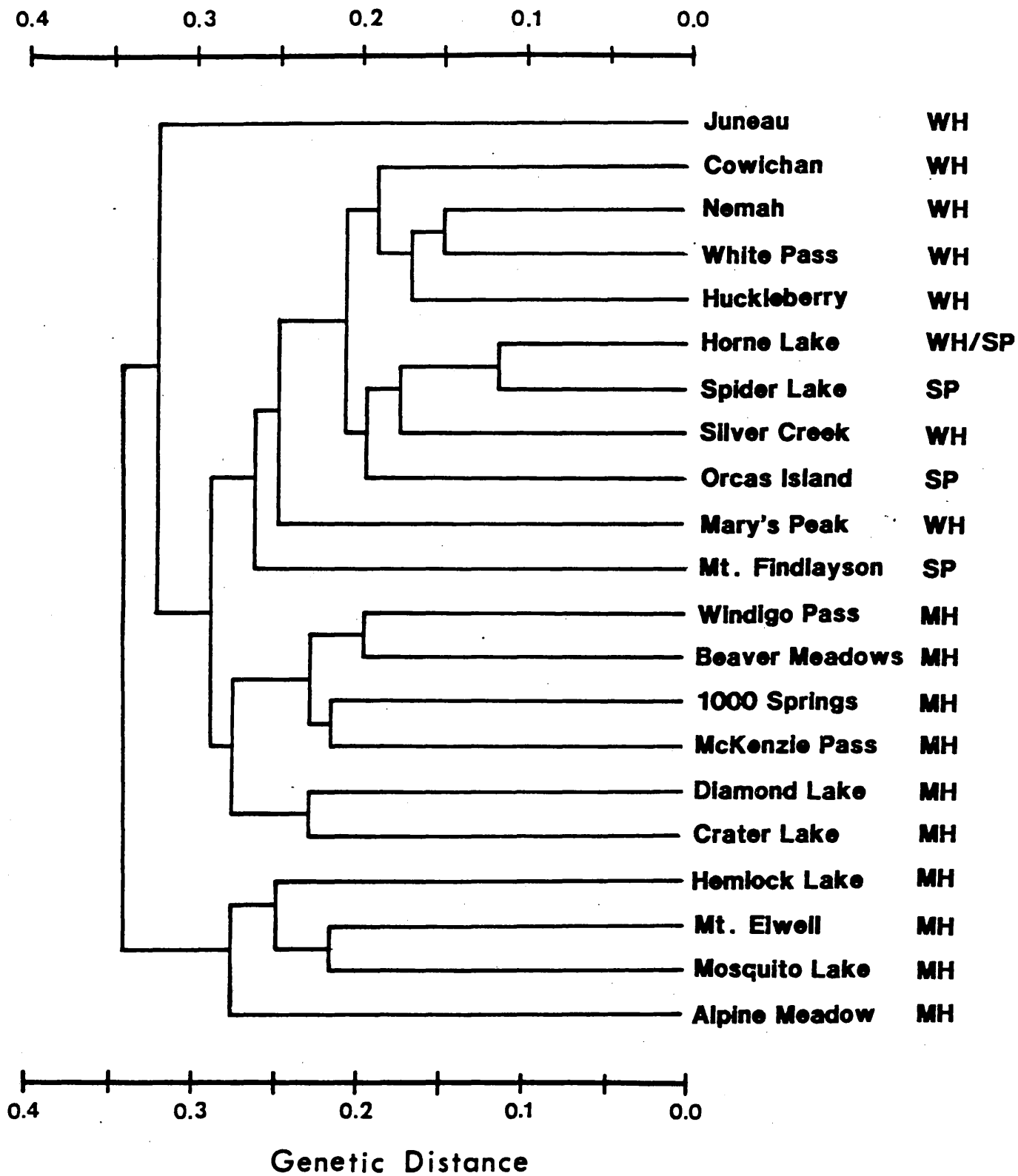
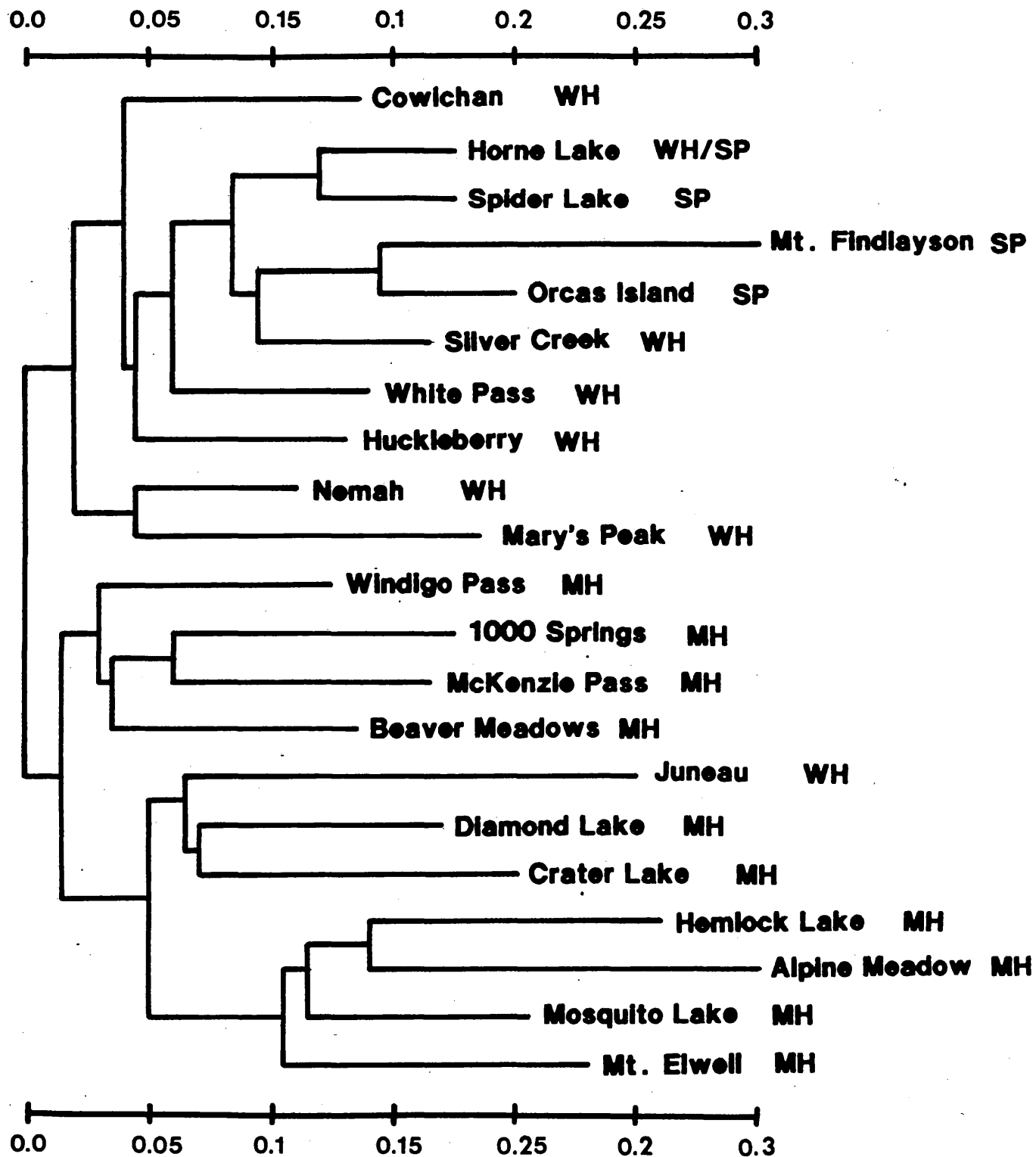


Figure 4



Appendix I. Specific Locality Information for A. tsugense Populations (see Table 2 for population names).

1. Shasta Co., CA. Parasitic on Tsuga mertensiana. Lassen National Park, near Hemlock Lake, along Rt. 89. T 30 N, R 5 E, Sec. 17. Nickrent 2187. August 22, 1986.
2. Plumas Co., CA. Parasitic on Tsuga mertensiana (Nickrent 2194) and Pinus monticola (Nickrent 2195). Plumas National Forest ca. 6.0 air miles SW of Graegle along trail from Lakes Basin Group campground to Mt. Elwell, near Silver Lake. T 21 N, R 12 E, Sec. 7. August 24, 1986.
3. Placer Co., CA. Parasitic on Tsuga mertensiana (Nickrent 2212) and Pinus monticola (Nickrent 2213). Tahoe National Forest, along the Roundhouse ski lift above the Alpine Meadow Ski Resort, ca. 5.0 miles west of Tahoe City. T 15 N, R 16 E, Sec. 18. October 17, 1986.
4. Alpine Co., CA. Parasitic on Tsuga mertensiana (Nickrent 2216) and Pinus monticola (Nickrent 2217). Toiyabe National Forest, along the south side of Mosquito Lake and along trail to Heiser Lake, ca. 6.0 miles northeast of Alpine along S.H. 4. T 8 N, R 19 E, Sec. 29. October 17, 1986.
5. Juneau, Alaska. Parasitic on Tsuga heterophylla. Along the Juneau road system. Collected by Paul Hennon and Elaine Loopstra (S.N.). October 21, 1986.
6. Vancouver Island, British Columbia, Canada. Parasitic on Tsuga heterophylla. Just outside the Cowichan Forestry Research Station gate, Lake Cowichan. Nickrent 2661. August 21, 1987.
7. Vancouver Island, British Columbia. Parasitic on Tsuga heterophylla (Nickrent 2663) and Pinus contorta (Nickrent 2664). Horne Lake Road, along north side of Horne Lake and along the north beach of Horne Lake, ca. 8 km SW of Qualicum. August 22, 1987.
8. Vancouver Island, British Columbia. Parasitic on Pinus contorta. Along the beach at Spider Lake, ca. 6 km S of Qualicum. Nickrent 2665. August 22, 1987.
9. Vancouver Island, British Columbia, Canada. Parasitic on Pinus contorta. Summit of Mt. Findlayson, just east of Rt. 1 and ca. 14 air kms. west of Victoria. Nickrent 2666. August 23, 1987.
10. Pacific Co., WA. Parasitic on Tsuga heterophylla. Along North Nemah Rd. that parallels U.S. 101 to Nemah. Nickrent 2667. August 29, 1987.
11. Lewis Co., WA. Parasitic on Tsuga heterophylla (Nickrent 2668) and Abies amabilis (Nickrent 2669). Gifford-Pinchot National Forest, just north of Goat Rocks Wilderness area, 4.0 miles NE of White Pass (unincorporated) along Rt. 12. T 13 N, R 11 E, Sec. 5. August 30, 1987.
12. Pierce Co., WA. Parasitic on Tsuga heterophylla. Mt. Baker-Snoqualmie National Forest at Silver Creek, around parking lot at information booth, just outside Mt. Rainier National Park. T 17 N, R 10 E, Sec. 3. Nickrent 2670. September 1, 1987.

13. Pierce Co., WA. Parasitic on Tsuga heterophylla. Mt. Baker-Snoqualmie National Forest at Huckleberry Camp (U.S. Army) road along F.H. 73, just off Rt. 410. T 18 N, R 10 E, Sec. 6. Nickrent 2671. September 1, 1987
14. Benton Co., OR. Parasitic on Abies procera. Siuslaw National Forest, on Mary's Peak near the microwave relay station, 0.7 miles W of the campground turnoff. T 12 S, R 7 W, Sec. 20. Nickrent 2673. September 8, 1987
15. Klamath Co., OR. Parasitic on Tsuga mertensiana (Nickrent 2674) and Pinus monticola (Nickrent 2675). Deschutes National Forest, 1.5 miles NE of Windigo Pass along F.H. 60. T 25 S, R 6 E, Sec. 28. September 9, 1987
16. Douglas Co., OR. Parasitic on Tsuga mertensiana. Umpqua National Forest, along Rt. 138, 1.8 miles N of jnc. with 230, just east of Diamond Lake. Intermixed with Pinus contorta infected with Arceuthobium americanum. T 28 S, R 6 E, Sec. 16. Nickrent 2676. September 9, 1987.
17. Klamath Co., OR. Parasitic on Pinus albicaulis (Nickrent 2677) and Tsuga mertensiana (Nickrent 2678). Palisade Point, along rim drive, Crater Lake National Park. September 9, 1987.
18. Jackson Co., OR. Parasitic on Tsuga mertensiana. Rogue River National Forest at Thousand Springs area, 3.0 miles SE of Rt. 62 along F.H. 800, 1.0 mile west of Crater Lake National Park boundary. Site hosts a diversity of conifer species including Tsuga heterophylla (no dwarf mistletoe infections seen), Pseudotsuga menziesii, Pinus monticola, P. contorta, P. ponderosa, Abies procera, A. lasiocarpa (one infected tree seen, Nickrent 2680), A. grandis, and Picea engelmannii. T 31 S, R 4 E, Sec. 12. Nickrent 2679. September 10, 1987
19. Douglas Co., OR. Parasitic on Pinus monticola (Nickrent 2681) and Tsuga mertensiana (Nickrent 2682). Rogue River National Forest along Rt. 230, 15.5 miles NE of Union Creek. T 28 S, R 4 E, Sec. 36. September 10, 1987
20. Lane Co., OR. Parasitic on Tsuga mertensiana (Nickrent 2684), Abies lasiocarpa (Nickrent 2685), and Pinus albicaulis (Nickrent 2686). Willamette National Forest, Washington Wilderness area, in volcanic rock zone 1.5 miles W of McKenzie Pass along Rt. 242. T 15 S, R 8 E, Sec. 19. September 11, 1987
21. San Juan Co., WA. Parasitic on Pinus contorta. Mt. Constitution (?), Orcas Island. Collected by F. G. Hawksworth (# ?), September, 1987.